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THE YUCCA PLANT, *YUCCA FILAMENTOSA*, AND THE YUCCA MOTH, *TEGETICULA (PRONUBA) YUCCASELLA* RILEY: AN ECOLOGICO-BEHAVIOR STUDY[1]

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Of all the delightful treatises in the field of natural history, none, I dare say, surpasses the one by Charles V. Riley on the life-history of the Pronuba moth and its relation to the pollination of the flowers of the Yucca plant. Observations and experiments on this relationship by Riley and the botanists, George Engelmann and William Trelease, covered a period of twenty years. During that long time, they repeatedly uncovered the intricate and almost unbelievable details of the behavior of the moths at the flowers, and often the work was conducted in the presence of friends and colleagues. Their findings may be verified to-day, by any one with a flashlight, during the blooming period of the plants.

Riley published short papers from time to time as the investigation progressed, and finally put the whole story together in the 'Third Annual Report of the Missouri Botanical Garden' in 1892, under the caption, "The Yucca Moth and Yucca Pollination." The paper is charmingly written, replete with beautiful drawings made by Riley himself, and is to-day regarded as one of the classics of natural history. This treatise points out to us that nowhere else do we find such hand-and-glove interdependence of flower and insect. Neither plant nor insect could perpetuate itself without the other, for the Yuccas depend solely upon the moth for pollination, and the larval moths in turn depend solely upon the ripening seeds for food.

In order to insure the development of the seeds so that the larvae may have food, the mother moth actually packs pollen into the stigmatic opening of the pistil. By this act she also accomplishes fertilization in a very difficult flower

[1] My specimens of the Yucca moth were kindly identified by Mr. August Busk of the U. S. Department of Agriculture. Other insects mentioned were identified by others whose names appear in brackets throughout this paper.

which cannot be pollinated by wind or by bees. Since the larvae eat only a small portion of the growing ovules, the plant enjoys the benefit of an ample crop of seeds.

The most striking part of Riley's paper, from the standpoint of insect psychology, is the behavior of the mothers at the flowers. However, from the standpoint of ecology and evolution, the most exciting part is the discovery that the short-lived, non-feeding moths come upon the scene simultaneously with the opening of the flowers, which also are short-lived—a perfect adaptation in time of each to the other. The origin of this adaptation has never been adequately explained. Like all problems which touch upon the fascinating subject of origins, it is difficult to investigate. I have, however, made a feeble attempt at such a study, as the later pages will show. I have also verified much of Riley's work, and in the course of observations have stumbled upon additional facts on the behavior and the ecology of both insect and plant.

Behavior of the Moth

First, let us review briefly Riley's discoveries on the interdependence of moth and flower.

The adult moths appear just as soon as the flowers open. Being silvery-white, they enjoy a marked amount of color protection when within the white flowers. The flowers have the most attraction during the first and second nights of their opening, probably because their fragrance is strongest at that time. The moths, small and delicate as they appear, are hardy and are strong fliers.

The mother, when ready to oviposit, gathers a ball of the sticky pollen from the anthers. In order to do this, she uncoils her tongue over the anther and stretches out to the fullest extent her maxillary tentacles. Then, by a series of forward and backward movements of the body, she scrapes the pollen with her palpi toward the tentacles. She goes from one anther to another, sometimes to as many as four, until she has a large load. This she kneads and shapes into a ball, and holding it firmly under her chin, she runs about until she finds a flower which is suitable for ovipositing. Having found one, she seeks a favorable point on the pistil and, thrusting her lance-like ovipositor into the soft tissue of the ovary, conducts the egg to its destination. No sooner is the ovipositor withdrawn than the moth thrusts a portion of her pollen-ball into the stigmatic opening and works her head rapidly "with vigor that would indicate pleasure and purpose" in packing it down. She makes every effort to force the pollen into the tube, often using her tongue to thrust it forward into the cavity.

The one load of pollen serves for several fertilizations. Each time she deposits an egg in the pistil, she repeats this process of cramming pollen into the stigma, and this is true of any subsequent eggs which are deposited in the same pistil—one fertilization for each egg deposited is the rule.

There is no other method by which larvae hatching from these eggs are assured of food, and Nature has provided no other means of pollination for this plant but this fantastic one. The behavior of the insect is all the more impressive when one remembers that she herself gets nothing at all from the flower. In fact, she has no means of imbibing food, and yet she goes through these intricate movements solely to supply, or rather to manufacture as it were, food for her young.

Riley was highly fascinated by the wonders which unfolded before his eyes, and he says:

> We have in the structures and functions which are so characteristic of this Yucca moth, admirable adaptations of means to an end . . . . . There is between Pronuba and its food-plant a mutual interdependence which at once excites our wonder, and is fraught with interesting suggestions to those who are in the habit of reasoning from effect to cause . . . . . The peculiar structure of the flower which prevents self-fertilization, though on a superficial view it strikes one as a disadvantage, is, in reality, a benefit, as the value of cross-fertilization has been fully established; while the maxillary tentacles of the female moth are very plainly an advantage to her species in the 'struggle for life'; and it is quite easy to conceive, on Darwinian grounds, how both these characteristics have been produced in the course of time from archetypal forms which possessed neither, and in reality we get a good insight into the process in studying the characteristics of other species of the family Prodoxidae. These peculiarities are, moreover, mutually and reciprocally beneficial, so that the plant and the animal are each influenced and modified by the other, and the same laws which produced the beneficial specialization of parts will maintain them by the elimination of all tendencies to depart from them.

The Yucca Plant and Its Flowers

The Pronuba moths are on hand during the very first evening that the flowers are open, and may be seen within the blossoms during the entire blooming period. Even at the end of the season, the last and only flower remaining on the stalk may be full of them. Flowers and insects appear as if by magic at the precise moment. If they did not do so, the perpetuation of both species would be defeated. This meeting at the right time is not an occasional coincidence, but evidently is the result of long years of "give and take", "come and go", and "trial and error"—natural selection at work eliminating year after year the offspring of one or the other that came upon the scene too soon or too late. Eventually the time period of both, in hand-and-glove fashion, became fixed in heredity, and the natural selection that brought on this condition of coincidental appearance maintained them by the same methods.

Before seeking to discover what influences are responsible for this coincidental appearance, one should first know something about the flowering habits of the plant. The flowers of *Yucca filamentosa* bloom in Missouri in June of each year, and remain open for only a short time. I have compiled in the table data on various aspects of the flowers' biology for nine consecutive years, 1934 to 1942 inclusive.

Year	1st flowers to bloom on author's terrace	1st flowers to bloom elsewhere in the neighborhood	Date flowers began to decline	End of blooming period	Number of flower stalks on plants on author's terrace	Number of days plants in flower
1934	June 5	———	———	———	———	———
1935	June 17	June 15	June 30	July 12	38	27
1936	June 6	June 4	———	———	———	———
1937	June 13	June 9	June 29	July 5	70	22
1938	June 4	May 31	June 22	June 30	53	26
1939	June 11	June 7	June 28	July 2	40	21
1940	June 13	June 11	June 27	July 2	58	20
1941	June 2	May 31	June 14	June 26	105	24
1942	June 2	May 30	June 19	June 29	28	27

The table shows that the flowers bloom from 20 to 27 days each year. The first flowers opened between June 2 and June 17, and the last flowers disappeared between June 26 and July 12, inclusive. The variations of the opening and closing dates, while apparently slight, are of vast importance, since the short-lived moths must, without fail, match this blooming period by their own appearance. This leaves us wondering what causal factors have sharpened Nature's mutual adjustment to so fine a point. Is this simultaneous development due to some environmental factors, such as early or late spring, wet or dry periods, sunshine or shade? And do these conditions influence in some way the flower-bearing stalks and the insects in the earth as well? If they do, it will go well with both, but if one or the other puts in its appearance too soon or too late, both flower and insect must die without leaving progeny.

The Yucca plants which grow on my terrace and are somewhat shaded by trees during part of each day, I regard as growing in semi-shade. There are also a large number of plants growing in a sunny open field near by. For a number of years, I have noticed that flowers appear on the plants in the sunny location earlier than they do on my semi-shaded terrace. In the third column of the table, you may see that the flowers bloom from one to four days earlier in the open sun than they do in the semi-shade.

On the other hand, in a heavily shaded estate not far from my home, I find the Yucca flowers appearing still later than those on my semi-shaded terrace. For example, in 1941 the plants on my terrace began to flower on June 2, and on June 8 had 105 stalks, 82 of which were then in flower. On June 8 I examined the stalks in the heavily shaded estate, and counted 25, none of which bore a flower. Two days later, June 10, all of the 105 stalks on the terrace bore flowers, and of the 25 plants in the heavily shaded garden, only five stalks had open flowers, and then only from one to three to a stalk. Another instance in point: On July 2, on the highway near DeSoto, Missouri, I noticed a large number of Yucca plants in a heavily shaded cemetery, all of which were in full flower; a mile down the road, however, in a sunny farmyard, a similar lot was all through flowering and all stalks bore large green seed-pods.

Thus we see the effects of three environmental situations—shade, semi-shade and sunshine—on the blooming propensities of Yucca. Sunshine and shade are undoubtedly factors, within limits of course, in regulating the appearance of Yucca flowers. Riley seems perturbed when he finds the Yuccas blooming two weeks later in Philadelphia than they do in near-by Washington. He says there appears to be some irregularity in the blooming time of these plants. Evidently, what he did was to observe one set growing in the sunshine and another in the shade. In the light of the behavior of our neighborhood Yuccas, sunlight and shade would account for the irregularity which Riley observed. He does not tell us if there was also a similar irregularity in the appearance of the moths.

The Stalk, the Flower and the Seed-pod

Before we go into the details of the regularity and irregularity of the appearance of the moths, we must have some knowledge of the day-to-day progress of the growth of the plant, especially the development of the flower-stalks, the opening of the flowers, and the ripening of the seed-pods. These details are interesting from the standpoint of flower ecology, and have some bearing on the life of the Pronuba moth.

Here, as an example, are the happenings on my terrace in 1941:

May 18. The flower-stalks, light-green, tender and asparagus-like, are pushing their heads up from the center of the plants.

May 27. They are now half-grown, and number 105.

June 2. 11:30 A. M. The flower-stalks are full-grown but bear no flowers. A careful search is made about the plants for any Pronuba moths that may be lying in wait for the flowers to open; none are found.

Same day, 10 P. M. Some time during the afternoon, 15 flowers have opened, and these are on four stalks. An examination at 10 P. M. revealed 52 Pronubas crowded into them. The temperature is 72° F. No moths were lurking about the plants or buds when I examined them at noon, and now there are within the flowers 21 males and 31 females. Their distribution is as follows:

					Males	Females
	2	flowers,	each	with	1	1
	1	"	"	"	4	4
	2	"	"	"	0	1
	1	"	"	"	0	5
	1	"	"	"	2	1
	5	"	"	"	1	2
	1	"	"	"	1	3
	1	"	"	"	3	1
	1	"	"	"	4	3
Total	15	"	"	"	21	31

June 3, 10 P. M. Three additional stalks now have flowers, and all of these harbor moths, some of which are in copula.

June 5, 10 P. M. A total of 30 stalks now have flowers, and almost all of them contain moths. Observing them until midnight, I find them nervously walking and flying about the flowers, evidently in search of newly opened ones that may not yet have served as a repository for eggs.

June 7. A total of 53 stalks now have flowers.

June 8. A total of 82 stalks now have flowers.

June 9. A total of 98 stalks now have flowers.

June 10. All 105 stalks now have flowers.

June 14. Some of the first stalks to bloom now have dead or discolored flowers, and also small, green seed-pods are beginning to form on several of them.

June 21. The first stalks to bloom are now in complete decline, but on the others, flowers continue to open.

June 23. The flowers on about 85 per cent of the stalks are rapidly declining, and some of them bear green seed-pods two inches long, thus giving evidence that Mother Pronuba has done her work well.

June 26. Only three stalks now remain that have flowers, and these total only eight. Three of these contain moths, probably newly emerged, for their wings are clean and fresh.

June 29. Only one flower now remains open, and it has attracted to itself a Pronuba, probably, too, the last one of the summer. So here ends the season of Pronuba moths and Yucca blossoms. They have appeared on the scene simultaneously, have played their brief drama strenuously, and now are no more, but the bountiful crop of green pods filled with ripening seeds and growing larvae assures continued life to both species.

July 7. The pods are large, and the seeds within them are ripening; the larvae are feeding on the seeds and are becoming large and fat.

July 16. Some of the pods show spots on the outside. These spots of discolored tissue thinly cover the exit holes in the pod-wall which were cut by the larvae in anticipation of their escape. This bit of foresight (if it may be so called) on the part of the larvae will be discussed later.

July 27. The green pods are rapidly turning brown and becoming hard, and the spots have now given way to full-sized openings from which the larvae are escaping and dropping to the earth.

August 13. The pods are becoming very tough, and the exit holes numerous, indicating that practically all of the larvae have emerged.

August 18. During the past few days, about 75 per cent of the pods have reached full maturity and have burst open, scattering the many seeds which were not eaten by the larvae. With the ripe seeds now disseminated over the surrounding earth, and a new generation of Pronuba babes snugly encased in silken cocoons in the ground, the activities of the whole year, all crowded into a few days, end, and for ten months life seems to have gone out. But with the advent of another summer the flowers and insects will spring into action *simultaneously* to repeat the drama.

The Adult Moth

The moths, as already stated, are to be seen within the flowers during the very first evening of their opening; they continue within the perianth during the entire blooming period of 20 to 27 days; and when one peeps into the last remaining flower at the end of the season he will be greeted by the disturbed moths flying into the air.

In the foregoing chapter the details of moth and flower relations for the year 1941 were given. Additional confirmatory notes are herewith presented.

In 1935, on June 16, there were 30 flower stalks on my terrace in bud, but a careful search about the plants revealed not one adult Pronuba moth. The next evening, three of the stalks bore flowers, within which 18 moths were counted. On the final day of their blooming, July 12, only one open flower remained, and crowded in it were 12 moths.

In 1937, on June 17, four days after the plants commenced to bloom, 243 flowers were counted, and the moths were estimated to number about 75; ten pairs of these were in copula.

In 1938, the first flowers opened on June 4. There were 14 of them on three panicles, and at 10 P. M. 55 moths rested within them. Some flowers harbored from five to ten, and others, of course, had none. The few remaining flowers at the end of the season, June 27 to June 30, all contained moths to the very end.

In 1939, the first flowers opened on eight panicles on June 11, and during the first evening each of them contained from one to four moths; during the last days of blooming, June 28 to July 2, there were moths in the few remaining flowers.

In 1941, on the morning of June 8, six days after the flowers had begun to open, I counted only five moths in 50 flowers. In the early afternoon, more flowers burst open, and the air was full of their fragrance. The small number of moths was perplexing, to say the least, but when I visited the flowers early that evening masses of silvery winged Pronubas were flying to the new flowers.

This gave me the first idea that the moths do not come up from the earth immediately surrounding the plant and walk directly up the stalk to select a flower by the sense of sight. They are without doubt attracted to the flowers by the sense of smell, and the reason I found only 5 moths in 50 flowers was that either the flowers were so old that they had lost their fragrance, or the wind was in the wrong direction or not strong enough to carry the news to the moths lying in wait somewhere. This subject will be enlarged upon later. It is strange that the fragrance of the flower should attract these insects, since for themselves food is not their goal. The object of the quest for the female evidently is a place where she may, in ichneumon-fly fashion, deposit her eggs, and the goal for the male in the flowers can only be the presence of the female. It is a complicated situation indeed if the male responds, not to the odor of the female, but to the odor of the flower she frequents.

The moths of both sexes, easily distinguishable, are short-lived and take no food, the tongue having lost its function. (In the laboratory the males lived two to three days, and the females three to five days.) They spend their adult lives within the full-blown perianth. Mating takes place there, and the pairs remain together facing in opposite directions for from two to four hours. When disturbed, they often walk about slowly without separating.

The behavior of oviposition is startling enough, but that of gathering pollen (is any other moth known to gather pollen?) and deliberately using it to impregnate the ovaries of the plant, thereby creating—instead of merely gathering—food for her young, seems as incredible, as one author puts it, "as a tale of Munchausen."

The aforementioned behaviors are mainly biological and psychological, but equally startling are the ecological facts connected with the simultaneous appearance of the moths and flowers. Has the plant adapted the time of the opening of its flowers to the appearance of the moth, or is it the other way around? Is the coincidence that we witness the "end stage" of a long series of steps of "give and take", "come and go", in the evolution of this phenomenon?

We know little of these steps, but we may some day discover them by the historical or by the comparative study of the near relatives of Pronuba. To digress for a moment, various not-far-distant relatives of Pronuba are given to many singular and astonishing ways of making a living for themselves and their young, and perhaps Pronuba has come by her eccentric habits honestly. To mention but a few of the queer things that her relatives do, one may cite the clothes-moths, the wax-moths, the fur-sloth moths, the cattle-horn feeders, the owl-pellet feeders, the pigeon-trash feeders. Some lepidoptera are even parasitic on bumblebees and wasps, and one species has even gone so far as to be an internal parasite of certain Coccidae. Being unwilling to wait until a study could be made of Pronuba's relatives, past and present, I proceeded to carry on experiments to see what external environmental conditions may be responsible for the delicate adjustment of insect to flower in point of time.

The Experiments

The larva, having completed its feeding within the Yucca pod, drops to the ground, penetrates the earth a few inches and spends the winter underground in a cocoon of silk that it has spun for itself. Late in the spring, a short time before the opening of the Yuccas, the larvae transform into pupae. The pupa is heavily armed with spade-like dorsal spines with which, at the proper time, it forces itself out of the earth. When on the surface, it speedily transforms into a winged moth ready almost immediately to pollinate the flowers.

Suspecting that the larvae may be influenced by temperature conditions, simple experiments were set up to learn what one could about it. The larvae, when full fed or nearly so, were removed from the pods and placed in tin cans with loose soil; they readily buried themselves in it. The cans were tightly covered but were aerated occasionally, and the soil was moistened four or five times during the winter.

Experiment I.—Several hundred larvae were placed in tin cans on July 28, 1937, and kept in a room during the winter where the temperature varied from 42° to 60° F. A careful record was kept of the dates the adults emerged the following spring, and are as follows:

1938		Number of moths
May	17–18	55
	19–20	21
	21–22	18
	23–24	36
	25–26	49
	27–28	5
	29–30	36
June	1	41
	3	3
	6	29
	7	8
	14	13
Total		314

The data are extremely interesting in connection with the dates of flowering of the Yuccas for that year. This period for 1938 was from June 4 to June 30, 26 days. Now we see in this table that three-fourths or more of the moths emerged too early to do the plants or themselves any good. If the moths in their natural habitat emerged in the same way, it would be woe to both insect and plant. Evidently the emergence was influenced by temperature conditions, and, as one would expect, the occasionally heated room (at least it was warmer than the outside earth in which the moths normally spend the winter) stimulated development, and the moths emerged too soon.

In 1941-1942 similar tests were made under different conditions.

Experiment II a.—This is a repetition of Experiment I, and was made solely for the purpose of serving as controls of Experiments II b and II c, to follow. The dates when the adults emerged and their numbers follow:

1942		Number of moths
May	19–20	6
	21–22	3
	23–24	10
	25–26	22
	27–28	14
	29–30	12
June	1–2	17
	3–4	8
	5–6	8
	7–8	5
	9–10	4
	18	1
July	1	1
	4	1
Total		112

Here the conditions were the same as in Experiment I, and the dates when the 112 adults emerged coincide very nicely with those in that experiment, except for two stragglers in July.

Experiment II b.—On the same day that controls were set up in Experiment II a, another one was set up as II b, with this important difference: the cans were kept outdoors in an open barn, where the temperature was practically the same as that outside. The conditions of this test are closer to those of the natural hibernating quarters of the moths in the earth, but still are not quite the same.

The dates of the emergence and the numbers were as follows:

1942		Number of moths
June	1–2	10
	3–4	16
	5–6	52
	7–8	43
	9–10	10
	11–12	4
	13–14	4
	15–16	2
	17–18	3
	19–20	2
	21–22	0
	23–24	3
	25–26	3
	27–28	2
Total		154

Thus 154 moths emerged from cans in the barn from June 1 to 28; 139 during the first half of June, and only 15 during the last half. By comparing these dates with controls kept indoors (Experiments I and I a) we see that temperature is a potent factor influencing emergence. The larvae that were kept in cans in the cold barn emerged in line with those hibernating in the earth, quite in time to pollinate the Yucca flowers.

The flowers that year were open from June 2 to 29, and the first moths to emerge from my experimental cans came on June 2. They kept emerging thus from day to day during the entire blooming period of the Yuccas, with not a moth overstaying the flowering period by even a single day. So well did this experimental emergence coincide with the normal emergence (and also with the opening of the flowers) that when my moths were liberated near the plants they joined their comrades on the flowers, as though they were "native here, and to the manner born."

Experiment II c.—This test did not turn out well, evidently due to bad technique, but is included here more as a matter of record than for scientific yield. At the time Experiments II a and II b were started, 411 larvae, in six cans, were buried a few inches below ground near the Yucca plants. The cans were covered tightly, but either because of too much moisture or the lack of air, the mortality was enormous.[2]

The cans were exhumed on May 20 and examined every day for emerging adults, but only five came to the top, and all from one can—one on June 9, 3 on June 13, and one on June 25. These dates were all in line with the flowering period of the plants, and indicate at least that the conditions in the ground differed very little from those in the barn.

As shown in these experiments, the influence of temperature on emergence gives us an answer, in part at least, to the question we must ask ourselves when noting the difference in blooming time for plants growing in sunshine and in shade. How can emerging moths meet this erratic blooming behavior? Reasoning by analogy from the experiments, the answer is that when low temperature or lack of sunshine retards the blossoms, it affects likewise the emergence of the moths. A portion of ground heavily shaded by trees would take a longer time to warm up than a portion in the sunshine. This would retard the moths in the earth to an analogous extent that the shady cool environment above ground retards the flowers. By the retardation of both to a similar extent, nothing is lost in the end, and flower and insect meet and function normally.

How the Moths Come to the Flowers

As has already been stated, no moths are to be found near the plants when they are in bud, even a day or two before opening, but moths are often abundant in the flowers during the first evening of their blooming. I have always suspected that the moths bury themselves in hibernation near the growing plants, emerge from the ground some time before the flowers open, and lie in ambush, as it were, ready to fly to them at a moment's notice. In these studies I have learned that the caterpillars wander about for some time before entering the earth, and later as adults they are attracted to the flowers (as the following details will show) by the fragrance carried on the wind.

In 1935 the first flowers, three in number, opened on June 17. It rained all day on June 18, and the temperature remained around 58–60° F., and no other buds opened. June 19, with the temperature about 60–62°, 84 flowers opened,

[2] The cans were filled three-fourths full of soil, but those in the room and in the barn, which could more readily be handled, were often aerated.

but up to 7 P. M., not a moth was to be seen within a perianth. When I returned at 8:30 P. M., however, I found the air filled with the silvery-winged moths flying to the newly opened blossoms, while many were already settled within them, and others were walking from flower to flower, evidently seeking something "just a little bit better." I returned again at 10 P. M., and found the flight over, and from one to four moths in more than a third of the flowers, many of them in copula. It is plain to see in this case that the temperature of the day before did not deter the moths, for it differed little during the two days, but rather the lack of odor upon the wind caused their delay. It is very interesting to note also that even though the fragrance was on the air all the afternoon, the moths waited until after dark to respond to it.

During the next few days I could not visit the flowers until 10 P. M. I found newly opened blossoms from day to day, with many moths crowded into them. But on June 25, I was on hand earlier and again saw the moths flying to the flowers as they had done a few days previously. They wasted no time hovering before the flowers, but flew directly to them with a display of much nervousness and settled into them at once. They are strong fliers for so small an insect, and with my flashlight I could see them coming from the south. It was unfortunate that I could not discover from what distance they flew.

Another bit of evidence that Pronubas fly to the flowers from a distance was noted in 1938. A lawn in the town was leveled and resodded. Without touching the Yucca plants on the place, the workmen removed several inches of surface soil, thereby destroying any Pronuba larvae that might be hibernating there. The plants bore an abundance of flowers the following summer, but later not a stalk among them had seed-pods.[3] In 1940, they also produced flowers and also many seed-pods. The moths that effected the pollination must have flown there from the population on my premises, the nearest supply, and that about 1,100 feet away. They evidently had followed the trail of odor borne by the wind. Why did they do so in 1940, and not in 1939? My answer is, reasoning from analogy,[4] that it is quite likely the wind was not favorable in direction or in strength for carrying the flower odor to the places where the moths were.

Riley says (l. c., p. 122): "I have often been struck with the power which the moth has of detecting isolated plants blooming for the first time remote from other plants . . . . a fact which indicates that, where abundant, in addition to her ordinary more sedentary duties, she takes long reconnoitering flights."

In summary, I may say that Pronubas fly against the wind on the trail of the fragrance of the Yucca flowers, where they proceed promptly to the business of egg-laying. Pronuba moths do not fly at all hours of the night, but only between 8:30 and 9:30 P. M. This rhythmic periodicity is also found in certain species of fireflies and certain Saturniid moths, each species having its own set period for flight some time between twilight and dawn. The Pronubas often run

[3] The flower stalks shrivel when the flowers are not pollinated.

[4] The sex attraction and rhythmic periodicity of Saturniid moths. Acad. Sci. St. Louis, Trans. **26**:81-221. 1929.

restlessly from flower to flower; when this occurs, it is because there are too few newly opened flowers at hand, and the old ones have lost their attractiveness. I have frequently seen a moth inspect several flowers before selecting one in which to oviposit. Riley says that the stigmatic opening closes when once eggs are deposited in the pistil; perhaps this is a sufficient signal for the moth to seek a favorable place to oviposit elsewhere.

Unlike other moths, Pronubas are not attracted to light. The lighted windows of my home, only 40 feet from the terrace, have never attracted them. Only when they escape in the laboratory, where the dazzling light is very near, do they circle around the electric bulb in a confused manner.

The Larvae

Like the adult Pronuba, the larvae are quite hardy and can stand a lot of rough handling. Riley likewise found them so, for he says:[5] "It is the hardiest larva I have had to do with, and will not only repeatedly mend its cocoon when it is cut or torn, but when extracted from it, will survive for months if kept in a tight vessel." More than that, I find that the panicles of seed-pods may be cut from the plant and transported in the automobile for long distances. During the shake-up, many larvae fall from the pods and may later be picked up from the floor of the car. When the more mature ones of these are placed in cans of loose dirt, they will develop into normal adults.

The tiny, white, newly hatched larvae feed upon the white ovules. As the seeds become larger and darker, the larvae too grow larger, fatter and more colorful, and finally when the caterpillars reach full growth the color is red, tinged with green.[6] They eat the tender centers of a row of tightly packed seeds, destroying from 18 to 25 in the process. The tough rims of the seeds are not eaten, but serve (closely packed together as they are) as a wall of the cell-like domicile while the larvae continue to eat their way through the compact row. In addition to being closely packed, the seeds are held together by strands of silk spun by the larvae, as well as by bits of excrement pushed to the far end of the tunnel. This makes a comfortable "cocoon" and is so tightly held together that the whole set of otherwise loose seeds may easily be removed as one mass.

In the darkness of its cell, the larva grows while it eats its way through its food-mass and enlarges its tunnel. But toward the end of its career, it exhibits a bit of behavior that seems to bespeak purpose as much as the adult action in pollination. When nearly mature, the caterpillar interrupts its feeding long enough to cut a hole in the outer wall of the pod to permit its later escape. It does this while the pod is still tender, and its jaws can crush the green tissue of the wall. If the caterpillar waited too long to bite this hole, the walls would be found to be too tough, and the insect would be entombed. This job neatly done, it resumes

[5] Sixth Rept. State Entomol. Mo. pp. 131–135. 1874.

[6] One sometimes finds full-grown caterpillars that are of a beautiful amethyst-green hue. In one lot of 80, three such were found. When they were brought to maturity, the adults differed in no perceptible way from the reddish-green ones.

its feeding.

This precaution, which so resembles foresight, is not the only commendable item of its behavior. When cutting this hole through the wall of the pod, it stops short when it reaches the thin green outer skin. Thus the hole is concealed from the outside, yet is easily broken when the larva is ready to emerge. This concealment of the hole might evade enemies, for birds occasionally break open the pods. But Riley says that the open holes permit moisture to enter, causing a growth of fungus which might be detrimental to the larvae.[7]

While normally the caterpillar eats the tender centers of its row of seeds, when it cuts the exit-hole for future use, it must, in order to reach the pod-wall, bite its way out through the outer edges of the row of seeds; also it must turn squarely at right angles to its habitual course. After these sharp digressions from its usual quiet life, it goes back to feeding. The little discs of skin, like tightly stretched drum-heads, covering the holes, often turn brown while the pod is yet green, and are tell-tale landmarks that point to a fat larva just beneath. The holes are small, and the fat larvae have to struggle to push through them when escaping. They do not just fall out of the holes, but wriggle through in what appears to be a painful ordeal, at last breaking the thin, outer skin of the pod as they come out.

After the larvae have dropped to the earth, they walk about for some time before burrowing into it. Those in the laboratory, when placed on loose soil, wandered about for several hours before crawling down into it. It was formerly thought that the larvae, falling from the pods, enter the ground near their own plant; but seeing the larvae busily crawl about in the cans of earth, and also later seeing the adults fly to the flowers from a distance, I concluded that the larvae travel some distance from the plant for hibernation.

Riley says that the larvae penetrate the ground five or six inches, but in my tin cans they went down into the loose soil from one to three inches. They spend the winter underground, and in the late spring they transform into heavily spined pupae. At a later propitious moment they work their way out of the ground, shed the horny covering, inflate the silvery wings, and are ready for the business of reproduction when the first fragrance of Yucca flowers permeates the air.

If the larvae are needed for experimental purposes, the pods must not be gathered too early, or the larvae will be underfed; on the other hand, if one waits too long, the larvae will have escaped into the ground. They should be gathered, as near as possible, just when they have finished feeding; and the tell-tale brown spots on the outside of the full-grown green pods indicate that feeding is nearly

[7] It is interesting to note that the larvae of the bogus Yucca moth, which has a common ancestral origin with Pronuba, behave in a similar fashion. They feed on the pith of the flower stalk, but before spinning a cocoon eat a passage-way to the outer covering of the stem. However, they leave intact the thin membrane on the outside, through which later as adults they escape. Those which emerged from dried stems gathered hereabouts proved to be, according to Mr. Carl Heinrich, *Prodoxus quinquepunctellus* Chamb., which he states is a synonym of *P. decipiens*.

over. If the caterpillars are taken before they are mature, the mortality will be great. In a lot of 300 larvae gathered too soon, there was a mortality of 95 per cent in my cans, while under similar conditions, in a lot carefully selected for complete feeding, 48 out of 50 larvae transformed into normal adults.[8]

Dates of the exodus of the larvae may vary slightly in different localities and in different years in the same locality. However, at Kirkwood, pods on about July 15–25 contain full-grown larvae, while perhaps ten days later, the holes will be open and the larvae gone. If the panicles are left on the stalk, the pods naturally dehisce. If they are brought into the laboratory, they harden prematurely, and this before the larvae within can provide the escape-holes. The larvae are then prisoners, but they spin cocoons around themselves in their tunnels of half-eaten seeds and spend the winter in that way. A lot was discovered one spring, after having spent the winter within the pods in my cold barn, and they were found to be in good condition. Later all became normal adults.

It is amazing that so few Pronuba moths are parasitized. With several thousand developing in the laboratory, not one parasite issued from them. It is not due to the fact that the larvae are distasteful, for I have fed dozens of them to Polistes wasps, which in turn fed portions of the meat to their larvae. They were accepted as food by larval ant-lions also.

The larvae are generally free from enemies, excepting for a bird occasionally breaking into a pod, or a mouse eating the larvae along with the seeds in the laboratory. However, Riley has found ants destroying the larvae in the ground.

The larvae live and grow in these apparently air-tight pods, and the number per pod varies. There is no relation between the size of the pod and the number of insects feeding within it. In 1937, near the end of the season I gathered 10 panicles bearing 316 pods. Dissecting the pods, I made a count of the larvae within them, with the following results:

Number of larvae in each pod	Frequency	Total number of insects
0	3	0
1	12	12
2	19	38
3	48	144
4	60	240
5	64	320
6	54	324
7	16	112
8	24	192
9	8	72
10	7	70
11	0	0
12	1	12
Total	316	1536

[8] The tin cans were about three-fourths filled with loose earth and covered with tin lids, but they were aerated and lightly moistened during the season.

The 316 pods harbored 1,536 larvae, or an average of nearly 5 per pod. But it is interesting to note that more than two-thirds of the pods harbored from 3 to 6 larvae. In an extreme case, one pod had 12 larvae, and in this pod every seed was destroyed. In each of the 15 pods containing 9 and 10 larvae, only a few seeds (from 6 to 15) remained uneaten. In most of the other pods, there remained hundreds of good seeds ready for dissemination.

An interesting item in the table is the fact that three pods containing seeds had no larvae in them. This was to be expected, since these three pods bore no constrictions. Riley has shown that the deposition of the eggs in the pistil is responsible for the constrictions in the middle of the maturing pod. If the constriction is slight, only one or a very few larvae is likely to be found within the pod; if it is deep, many may be expected. Riley was able completely to eliminate the constrictions by pollinating the flowers by hand.

Riley found also, and my observations substantiate this, that no other insect is able to pollinate the Yuccas, since pollination requires that the sticky pollen be tightly packed in the stigmatic opening.

Of the 316 pods here examined, only 3 bore no larvae, and these had no constrictions. In the light of Riley's observations, my only explanation is that either the mother's ovaries were depleted, in spite of which she packed the stigmatic opening with pollen, or her instinct went so far astray that she packed her little bundle of dynamite into the stigma but omitted to place the egg in the pistil. Similar miscarriages of instinct often occur among the solitary wasps, where plentiful food is provided for the young and the egg is not deposited.

Insects Other Than Pronuba Taken on the Plants

Riley presents a list of several other insects which are to be found about Yucca flowers and plants.[9] He found positively that these insects had no hand in the pollination of the flowers; that office is performed by *Pronuba yuccasella* alone. I have found other insects about the plants, and I also have ascertained that these have no part in the transfer of pollen. A list of insects and their behavior follows, and I should like to mention that only three of my records are the same as Riley's; these three are marked with an asterisk.

BEETLES[10]

**Carpophilus melanopterus* Ev. [E. A. Chapin]. These beetles were present each year, and sometimes six or eight were to be found in one flower. Sometimes they shared a flower with several Pronubas. They were present during the entire blooming period of each year, but especially they were noticeable in the very first flowers on the night of their opening, and often did damage by eating portions of the pistil or by biting their way into the very heart of the unopened bud.

Obrium maculatum Oliv. [W. S. Fisher]. Only one beetle of this species was taken; it was on the outside of the flower on June 25, 1937.

[9] Footnote in Fifth Rept. Insects Mo. p. 154. 1873, and in Amer. Assoc. Adv. Sci. **29**:626. 1880.
[10] Names in brackets are those of persons who identified the insects.

Anthobatula trifasciata Melch. [H. S. Barber]. Only one specimen of this rove-beetle was taken; it was inside a flower, June 25, 1937.

**Chauliognathus pennsylvanicus*. The Pennsylvania soldier beetle was found each year about the leaves and within the flowers.

Coccinella novemnotata Hbd. [E. A. Chapin]. During the blooming season of 1935, many of these beetles, some of them in copula, were on the flowers. They were present on the stalks before the flowers opened, and remained through the blooming season.

Coleomegilla fuscilabris Muls. [E. A. Chapin]. One beetle seen on an unopened flower bud.

Trichiotinus piger F. [E. A. Chapin]. Only one of these Scarabidae was taken; it had its head deeply buried in a Yucca flower.

PLANT-LICE

Plant-lice, *Aphis rumicis* L. [P. W. Mason], are always abundant each year on the green flower stalks, although some years their numbers are much reduced by the aphis-lions. They usually collect on the bracts before the buds open and remain on them long after the white petals have fallen, often damaging the unopened buds. They feed on the juices of the plant, and appear to be just as abundant at the beginning of the season as at the end. They are often attended by the ant, *Formica fusca* var. *subserica* Say [M. R. Smith].

ANTS

When the tender flower stalks thrust up their asparagus-like heads, and later when the flowers are in bloom, one may often find aggregations of *Formica fusca* var. *subserica* Say upon them. They no doubt have been attracted to the plants by the plant-lice, but they have also been seen licking the exudations from the unopened flower buds.

Two other species of ants, *Monomorium minimum* Buckley [M. R. Smith] and *Penolepsis (Nylanderia) pavula* Magr. [M. R. Smith], were often seen on the flower-stalks, but what their interests on the plant were has not been ascertained.

APHIS-LIONS

The aphis-lions, *Chrysopa nigricornis* Bur. [A. B. Gurney], appeared in great numbers during certain years. At such times the plant-lice were greatly reduced. The females have often been observed depositing their stalked eggs on the plants at night.

HONEYBEES

*Honeybees, *Apis mellifica*, are always to be found about the flower-stalks, but they are seldom inside the blossoms. They usually content themselves with gathering the excretions on the outside of the base of the flowers. When they lap up the invisible excretions with protruding tongue, their abdomens pulsate rhythmically.

FLIES

Syrphus torvus O. S. [C. T. Greene]. These flies were often seen in company with the honeybees, lapping the exudations at the base of the flowers and also from the outside of the petals. Sometimes they fall prey to the flower spider, *Misumenops asparatus* Hentz. [E. B. Bryant], which often hides among the petals.

Allograpta obligua Say [C. T. Greene]. This fly was taken from the jaws of the above-mentioned spider in the center of a flower.

LEPIDOPTERA

Peridroma margaritosa Haw. [Carl Heinrich]. A caterpillar of this Noctuid species was seen eating into a flower-bud.

BUGS

Lygus pratensis oblineatus Say [H. G. Barber]. Occasionally a bug of this species was seen feeding on an unopened flower-bud.

Lopidea instabilis Reut. [H. G. Barber]. Seen occasionally feeding on flower-buds of the plant.

Leptocoris trivittatus Say [H. G. Barber]. A few nymphs taken from the plants during the blooming period in 1939.

Halticotoma valida Reut. [H. G. Barber]. This insect, known as the Yucca bug, has appeared on the plants on my terrace in such numbers during certain years as to injure them and reduce the number of flower-stalks. During 1939, only 40 flower stalks appeared (against 105 in 1941), and the flowers on each stalk were very few. Not one blossom was free of the bugs. Their sucking also produces numerous spots on the leaves, and not a leaf was free of these spots.

This enormous population in 1939 was evidently due to my having neglected to remove the fallen leaves that had accumulated about the plants for two years. The plants, however, recovered quickly when the accumulated debris was destroyed and the bug population thus reduced. After this had been done in 1940, the flower-stalks in 1941 numbered 105, all of which flowered heavily. The infestation appeared only on my neglected plants; other plants in the neighborhood were not noticeably infested. The bugs evidently find favorable winter quarters among the dead leaves, and spend their entire summer lives on the Yucca leaves, for in 1939 they were as abundant in October as they were in May.

Interpretations of Pronuba's Behavior

From the standpoint of comparative psychology, the behavior of Pronuba is of outstanding importance, and many students of behavior have sought in one way or another to explain the thorny problem of her actions. For example, McDougall[11] captions his discussion of the subject "Purely Instinctive Behavior," yet he is far from clear in throwing any light on the matter of the origin of these instincts. After describing the behavior of the moth at the flower, he says:

> Nature has so constituted the moth that she performs this cycle of nicely adjusted actions, essential to the continuance of the species, shortly after emerging from the chrysalis, when

[11] Outlines of psychology. pp. 74, 76. 1923.

she cannot have acquired any knowledge of the flower or of her grub and its needs. This is a fine example of the working of a chain instinct. Each step in the train of action brings the moth into a new situation in which new stimuli affect its sense organs. Why not be content to suppose, with the mechanists, that each step is simply a reflex action to some new stimulus . . . . . Consider a single step in this behavior, the placing of the egg in the one position in all the world where it can develop, this is among the ovules of the flower. Even if we assume that odor emanations from the ovules exert some tropic influence on the moth, it is obvious that this will not suffice to determine the placing of the egg in the right spot. That can be effected only under the guidance of a multitude of simultaneous and successive sense stimuli; and these must be not merely summated but rather synthesized and related to an appreciation of the shape of the parts of the flower concerned. In other words, the response of the moth to the flower is a perceptual response, not a mere reaction to a stimulus.

When one tries to find the meaning of "perceptual response" in his book, one is referred in the index to "Perceptual response to instinct" on page 99, but there we read the meaningless jargon which runs as follows:

Instinctive activity is normally initiated by an activity of perception, more or less complex; the capacity for this activity is given in the innate constitution of the animal, and is an essential part of the total instinctive disposition (or instinct) as the capacity to execute the train of bodily movements which catch our eye.

It seems to me, however, that if the action of the moth is a *perceptual response,* then it is not an instinctive one, but rather more or less akin to discriminating behavior. Fearful of crediting Pronuba with psychic attainments of too high an order, McDougall, in my opinion, gets nowhere in his attempt to explain the insect's behavior.

Wells, Huxley and Wells likewise take a shot at Pronuba's behavior, and are likewise parsimonious in interpreting her actions in ovipositing. They say:[12]

The impossibility of there being knowledge behind instinct is perhaps most prettily illustrated in the well-known case of the yucca plant and its moth, *Pronuba* . . . . . The association is one of mutual benefit, a reproductive symbiosis; the action of the female moth in putting the ball of pollen on the pistil seems admirably purposeful, just as her care not to kill the goose that lays the golden eggs, by only introducing three or four grubs into each flower-capsule, seems admirably calculated. But when we reflect that the mother moth dies before the seeds mature, and that the moths of the next generation have never seen a yucca in flower before they began their business of pollen-gathering and egg-laying, it becomes obvious that foresight and reason can play no part in the instinct—quite apart from the fact that experiments have decisively shown that no insect is capable of drawing such conclusions as the moth would have to draw if it were really being intelligent on the facts presented to it. We have no more right to suppose that the moth is being purposeful and intelligent in its actions than the yucca is being purposeful and intelligent in growing a pistil with a cup at its tip to receive the pollen; or, to confine ourselves to the moth, we have no more reason to find proof of intelligence in its actions in putting the yucca pollen in the proper place than in its growing the special appendage with which to manipulate the pollen.

Their parsimony goes still further when they say an instinct "is the outcome of the animal's nervous construction, as the leg and its working is the outcome of its mechanical construction. It is a bit of nerve-clockwork."

The statements by Wells, Huxley and Wells have the advantage of logic, but also the limitations of laboratory study. The authors go as far as they can in the generality that an instinct is the outcome of the animal's nervous constitution (which may or may not be true, because for all we know, the animal's nervous

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[12] The science of life, p. 1153. 1929.

constitution may be the outgrowth of its psychic life, just as the mechanical construction of its leg may also be the outcome of its movements), but that is beside the point, since they have said nothing to bring us any nearer to an understanding of how all this came about.

Riley, on the other hand, takes a more magnanimous view of Pronuba's psychic qualities. He goes quite far in his anthronomorphic explanation, which is probably the result of his having spent twenty years observing the behavior of these silver-winged moths in the field:

> The pollen grains would not adhere by chance to the rolled-up tentacles, and we have seen how full of purpose and deliberation Pronuba's actions are. It may be that all her actions are the result merely of "blind instinct", by which term proud man has been wont to designate the doings of inferior animals; but no one can watch her operations without feeling that there is in all of them much of purpose . . . . . Nor can I see any good reason for denying these lowly creatures a degree of consciousness of what they are about, or even of what will result from their labors. They have an object in view, and whether we attribute their performances to instinct or to reason depends altogether on the meaning we give to those words. Define instinct as "congenital habit" or "inherited association" or, as I prefer to characterize it, as *the inevitable outcome of organization* [italics Riley's] and most of the doings of the lower animals may justly be called instinctive; but the instinctive and reasoning faculties are both present, in most animals, in varying proportion, the last being called into play more especially by unusual and exceptional circumstances, and the power which guides the female Pronuba in her actions differs only in degree from that which directs a bird in the building of its nest, or which governs many of the actions of rational man.

Coquillet, to quote from Lovell[13], is even more positive than Riley, for he regards the behavior of Pronuba as a purely intelligent act, saying: "There appears to be no doubt that she is in possession of the fact that unless she did thus pollinate the flower, there would be no seed pods for her offspring to live on."

Riley, as you have seen, grants to Pronuba a higher degree of psychic ability, and he does so evidently because he repeatedly observed how full of purpose and deliberation her actions are; but when he, as well as Coquillet, credit the moths with a consciousness of what will result from their labors, they merely indulge in a guess, for who can know what goes on in the heads of these creatures!

However, one must admit that there are in the insect world numerous analogous cases where the participants likewise act as if they knew, and knew very well, what would be the end result of their labors. Whenever I see Pronuba deliberately pounding the pollen into the stigmatic opening, other brilliant behaviors come to my mind. Who can deny, for instance, that the Empis fly does not realize to what purpose he dances before the female with the marriage offering of a captured may-fly which she is to suck during the process of mating; or who will doubt that the queen bumblebee has some consciousness as to what purpose she broods her eggs when, hen-like, she keeps them warm day and night until they hatch; or the male butterfly of the genus Belenois[14] to what purpose he strokes the wings of the desired mate; or the saw-fly, *Perga lewisii*[15], the end for

[13] The flower and the bee. p. 144. 1918.
[14] Carpenter, G. D. H., A naturalist on Lake Victoria. p. 223. 1920.
[15] Carpenter, G. D. H., The biology of insects. Chap VIII. 1928.

which she strives when she watches over the eggs and later follows the young about as they feed, often covering them with her body to shield them from enemies and protect them from the sun; or the earwig, *Anisolabis mortima*,[15] when she cleans her eggs by rolling them in her mouth, and watches and guards them, as well as the young, when they are born; or does the bug, *Aepophilus bonnarei*,[15] when she gives the warning taps with her antennae which sends her young scampering for cover; or certain agricultural ants when they carry in their jaws on their marriage flight a pellet of fungus to start new gardens? And I cannot but recall my own observations on the intricate behavior of cockroaches,[16] in depositing and concealing their egg-cases. Many other examples could be cited.

But even if it is true that Pronuba's behavior is purely instinctive, we must admit that it could not possibly have always been so, for even an instinct must have had a beginning at some time. There is a first time for everything, and in the vast sweep of evolution, somewhere, sometime, certain especially endowed individuals, perhaps spurred to frantic exertion by some life-and-death stress, made unusual use of their faculties and adopted new ways with the flowers. The fact that a species performs a highly complicated and effective course of action, even though that course of action may now have become crystallized into instinct, points clearly to a line of progenitors who were versatile and were not afraid to try something new. It is an especially significant fact that relatives of this moth display an astonishing variety of outlandish accomplishments (mentioned elsewhere) which would justify our contention that the little Pronuba came from an "Edwards family" and not a "Jukes" in the insect world.

One may say in conclusion that if we wish to accord to present-day Pronubas a grain of intelligence, it is with the understanding that a great part of their actions are based on a well-developed set of instincts which were probably acquired bit by bit through the ages. On the other hand, branding their behavior as instinctive does not by any means preclude an ability occasionally to mix with it a bit of original variation, or a grain of something akin to intelligence. It may even require a modicum of intelligence to know when and where to make the best use of an equipment of instincts.

The Evolution of the Interrelationship

Both Yuccas and Pronubas, says Dr. William Trelease[17], are undoubtedly of recent geological origin; and the progenitors of the Yucca originally had spreading stigmas, and were also slightly entomophilous flowers pollinated by hymenoptera, diptera, or lepidoptera, which were attracted by the secretion of the septal nectar glands.

> With the consolidation of the stigmas, however, insects visiting the flowers for this nectar became inefficient pollinators, as may be seen when such insects enter the flowers of the existing Yuccas for the little nectar that is still produced; hence, with an economic reduc-

[16] See article, "How the cockroach deposits its egg-case; a study in insect behavior." Ann. Ent. Soc. Amer. **36**:221–226. 1943.

[17] Ann. Rept. Mo. Bot. Gard. **4**:217. 1893.

tion of the secretion of these glands, may have come an addition to their function to that normally borne by the stigma, in an increase in its secretion, so that the visitors, laden with pollen unconsciously accumulated while on the flower, should further visit the stigma on which some of their burden might be rubbed while they were feeding. During this stage of its evolution the plant appears to have proved especially attractive to some small moth, perhaps fond of nectar, and with phytophagous larvae, which is to be regarded as the progenitor of the Pronubas. . . . .[18]

Riley, too, agrees that Pronuba and Yucca have arisen from simpler forms, for he says.

The peculiar structure of the flower . . . . prevents self-fertilization; . . . . while the maxillary tentacles of the female moth are very plainly an advantage to her species in the "struggle for life"; and it is quite easy to conceive, on Darwinian grounds, how both these characteristics have been produced in the course of time from archetypal forms which possessed neither. . . .[19]

Since the structure of the insect has undoubtedly changed in the course of evolution, it is quite obvious that psychic changes have likewise occurred, and perhaps, after all, the brain and the mind of the free-flying Pronuba have played a more important role in the evolution of this singular relationship than has the brainless, immovable plant, which at most could have played only a passive role.

One can hardly assume that this mutual adaptation was a general merry-go-round process through the ages, each contributing equally to the other. The flower in the shadowland of its evolution could do no more than sway in the wind and abide its time, even as it does to-day. It had no choice in the selection of insects to perform the marriage rite, and could do no more than shed its fragrance on the passing breeze, and thus advertise its charms. The quality and condition of its charms, no doubt, varied over countless millenniums, and the insect was often compelled to choose or consciously select from among several variants.

The flower's important charms, in so far as Pronuba's behavior is concerned, are the stigma, the pollen, and the pistil, and from diversifications in these it had to select, for example: the stigmatic opening best suited to its pollen-pounding tongue; the pollen, dry, wet or moist, best suited to the carrying capacity or to the manipulating ability of its jaws; and the pistil best suited to the penetration of its peculiar ovipositor. In short, the blossom is selected by the insect and not the other way around. Pronuba has, in hammer-and-anvil fashion, hammered, let us say, the Yucca flower into what it is to-day, and the insect itself, in so doing, has undergone numerous changes—psychological and otherwise.

The Yucca apparently, as already suggested, has played but a minor part in the creation of the novel relationship, but a very important part, nevertheless—for if there were no Yucca-like flowers ever, there would not be (nor could there possibly be) the unique creature which we know to-day as ***Tegeticula (Pronuba) yuccasella.***

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[18] *Ibid.* p. 219.
[19] Ann. Rept. Mo. Bot. Gard. 3:126. 1892.